

FRANCES'S SPARROWHAWK *ACCIPITER FRANCESIAE* (AVES: ACCIPITRIDAE) RADIATION ON THE COMORO ISLANDS

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ABSTRACT

The nominate subspecies of Frances's Sparrowhawk *Accipiter francesiae* lives on Madagascar, while three of the Comoro Islands have distinct subspecies. Morphological variation among these four populations is peculiar: whereas on Madagascar a sexual difference in color pattern occurs, plumage differences are small in the Comoros populations, with masculine females (on Grand Comoro, Anjouan) and feminine males (on Mayotte), and there is also a juvenal plumage (*sensu* Palmer 1972) on Mayotte which does not exist in any other population. The Comoran endemics also show important differences between islands in density and habitat preference. DNA sequence analysis of the mitochondrial cytochrome oxidase 1 gene shows that they are characterized by closely related but distinct mitochondrial haplotypes. Furthermore, the phylogeographic pattern indicates that these islands were colonized in the same historical timeframe. We cannot date this event as yet, although considering the age of the archipelago (*c.* 3.9 Myr) it must have been relatively recent. The discrepancy between molecular and ecological results indicates rapid, divergent morphological and ecological evolution of the insular populations.

Key words: Madagascar, Comoros, cytochrome oxidase 1, Aves, Accipiter, phylogeography.

INTRODUCTION

The Comoro Islands are situated on a NW-SE axis between the African continent and Madagascar. The archipelago consists of four large volcanic islands (Grand Comoro, Moheli, Anjouan, and Mayotte; see geographical position on Fig. 1), and was never connected to any of the two neighboring old land masses. Volcanic activity is still ongoing after a complex history (Emerick & Duncan 1982). Grand Comoro is dated at 0.5 Myr BP (Nougier *et al.* 1986). This date corresponds to the oldest age that would allow the colonization by birds (Pasquet *et al.* 2007) but the three other islands are *c.* 3.9 Myr old (Nougier *et al.* 1986). However, island-hopping and local extinctions could have occurred more recently.

The present-day avifauna of the Comoros comprises 59 breeding species and approximately 49 species of migrants and vagrants; 17 species are endemic and another 19 breeding species are shared with Madagascar (and are absent from the African continent) (Louette *et al.* 2008).

One case of the latter category is Frances's Sparrowhawk *Accipiter francesiae* (for the nomenclature we follow BirdLife International 2009), a mainly reptile-eating raptor, the nominate subspecies of which lives throughout Madagascar. It also occurs on three of the four Comoro Islands (it is absent from Moheli), where it is the only representative of the raptor genus *Accipiter*. It is clear from morphological and ecological differences that populations are resident and isolated. Based on their morphology, the populations on each of these islands are thus considered as different subspecies (Benson 1960, Louette

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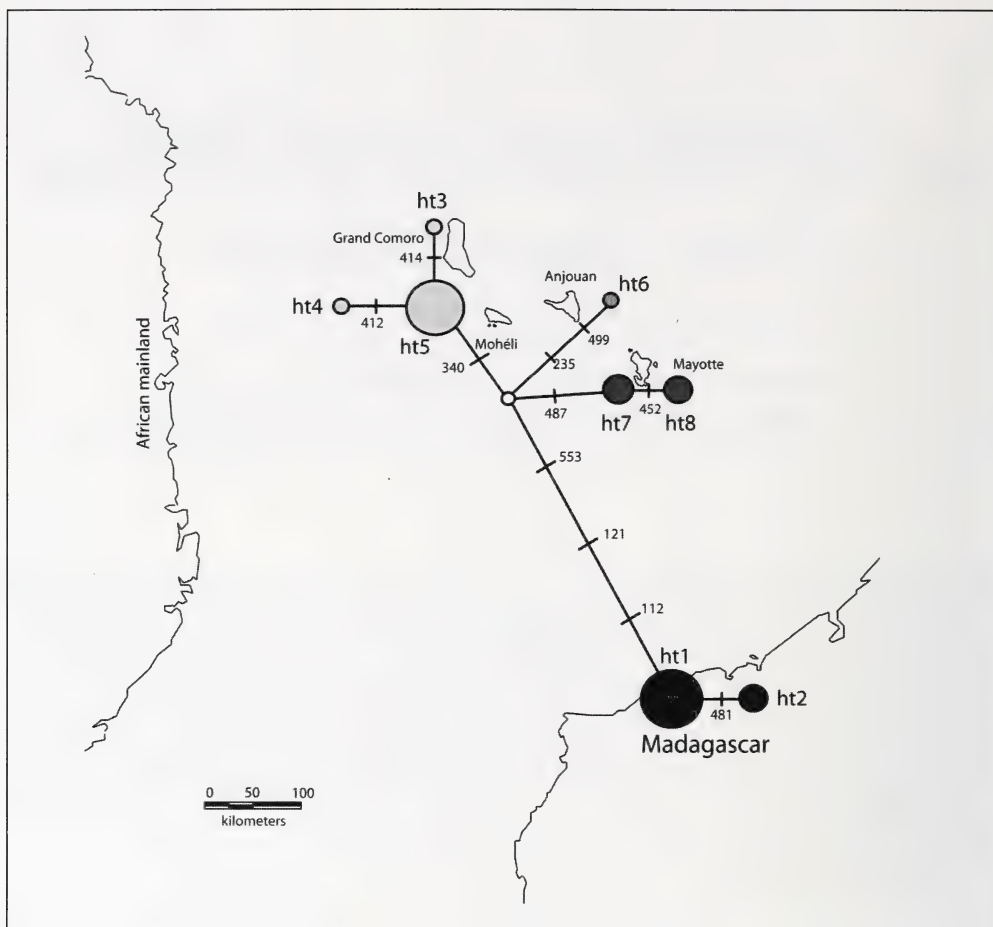


FIG. 1. Median-joining network of the eight haplotypes (ht1-h8) of *Accipiter francesiae* superimposed on a map of the Comoros and Madagascar. Circles (i.e. haplotypes) do not represent geographical sampling coordinates (see Table 1 for the coordinates). Numbers indicate nucleotide substitution positions and perpendicular lines indicate one nucleotide substitution in the COI sequence. The open circle represents a hypothetical ancestor for the Comoran subspecies.

1988, Ferguson-Lees & Christie 2001). It is assumed that the three Comoran taxa are derived from Madagascar stock (Louette 2004). Sexes on Madagascar (*A. f. francesiae* Smith, 1834) have well-differentiated plumages. Adult males are dark gray above with a paler head, the underside is white and thinly barred rufous to gray-brown on breast and upper flanks. Adult females are larger and browner above than males, with broader and much more profuse barring below. Juveniles resemble the female but are a richer and more rufous-brown above, and have

broader and browner bars below. The sexual dimorphism in plumage pattern is much less pronounced in the three Comoran subspecies, which are also slightly smaller than *A. f. francesiae* (del Hoyo *et al.* 1994, Herremans *et al.* 2001, unpublished data from ML: material at NHM, Tring, UK). On Grand Comoro (*A. f. griveaudi* Benson, 1960) and Anjouan [*A. f. pusillus* (Gurney, 1875)], *A. francesiae* is morphologically similar to male *A. f. francesiae*, in both sexes. The subspecies from Grand Comoro has a salmon flush on the breast. In the subspecies from

Anjouan the contrast of black and white plumage is particularly strong (Benson 1960, Ferguson-Lees & Christie 2001). On Mayotte, in *A. f. brutus* (Schlegel, 1866), both sexes resemble the female of the Malagasy subspecies in having brown upperparts and in being heavily barred brown underneath (Ferguson-Lees & Christie 2001, Herremans *et al.* 2001). *A. f. brutus* has a juvenal plumage which does not exist in any other population (Herremans *et al.* 2001, Herremans *et al.* 2011). Compared to the nominate form from Madagascar, *A. f. brutus* on Mayotte is thus partially neotenic (Herremans 1990). A relationship between neotenic evolution (reflected for example in plumages) and reduced territoriality and increased densities has been shown on the Comoros as one of the “insular syndromes” shared by several bird species (Louette *et al.* 1993).

The foot apparatus of a mainly reptile-eating *Accipiter* species has the peculiarity of a short middle toe (Wattel 1973). The Comoro birds differ in having a somewhat longer middle toe which is, relative to tarsus length, in *A. f. griveaudi* males 0.48, females 0.54; in *A. f. brutus* males 0.51, females 0.49; in *A. f. pusillus* males 0.54, females 0.55, compared with *A. f. francesiae* on Madagascar: males 0.43, females 0.44 (calculated from Rene de Roland & Thorstrom 2003, Herremans *et al.* 2011, and new calculations from measurements in the NHM by ML). These figures are still very much within the “normal” values for reptile-eaters (Herremans *et al.* 2011).

Bill length has also changed somewhat after the colonization process. Bill length (to cere) relative to wing length is in *A. f. griveaudi* males 0.090, females 0.090; in *A. f. brutus* males 0.089, females 0.091; in *A. f. pusillus* males 0.092, females 0.094 (calculated from Herremans *et al.* 2011, and new calculation from measurements in NHM by ML), compared with *A. f. francesiae* on Madagascar: males 0.085, females 0.088 (calculated from Rene de Roland & Thorstrom 2003). A long bill is a specialization for forest habitat, according to Wattel (1973).

Apart from the morphological differences, these subspecies also show remarkable differences with respect to habitat preference and population densities. The Malagasy race occurs “fairly commonly in various original forest types and degraded woodlands... from sea level to 2000 m” (Langrand 1990). On Mayotte, *A. francesiae brutus* prefers degraded habitats and attains record breeding densities in the agricultural landscapes of the western part of the main island at moderate altitudes (Herremans *et al.*

2001), whereas on Grand Comoro *griveaudi* is curiously restricted to the rainforest belt on the flanks of Mount Karthala and the immediate adjacent zones with lush vegetation, being absent from the northern volcano, La Grille (Louette *et al.* 2008). On Anjouan, due to the heavy degradation of the original vegetation, it is difficult to say which habitat is preferred, but all recent observations are from the central part of the island (Louette *et al.* 2008).

The species is the most common *Accipiter* on Madagascar (Langrand 1990, Rene de Roland & Thorstrom 2003) occurring throughout this large island, but is rarer in the xeric south. Whereas the subspecies *brutus* is numerous on Mayotte, with an estimated number of 7225–10 960 breeding pairs on less than 350 km² (Herremans *et al.* 2001), the subspecies *griveaudi* is restricted to an area of c. 400 km² on Grand Comoro. Although still “relatively common” it reaches only c. 10% of the density shown by *brutus* in prime habitat on Mayotte (Herremans *et al.* 2001, Louette *et al.* 2008). The subspecies *pusillus* on Anjouan is “rare” in an area of c. 200 km²; at one time it was even thought that this subspecies was close to extinction, but there are signs of recent recovery (Louette *et al.* 2008). It is possible that these differences in numbers between the islands are due to differences in the level of human persecution between the islands and not necessarily to intrinsic differences between the taxa. We do know that the species commonly uses exotic trees in open positions for nest building on Mayotte; in contrast, on Grand Comoro the only two nests ever found were built in closed forest at moderate altitude, and no nest has ever been found on Anjouan, which no doubt indicates that all nests are built in closed forest on those two islands (Herremans *et al.* 2001).

Here, we study the phylogenetic relationships between the different subspecies of *A. francesiae*, using the mitochondrial cytochrome oxidase 1 gene (COI) to elucidate their colonization history. In order to have a clue to the relationship with close relatives, we include in our analysis two other reptile-eating *Accipiter*, the Levant Sparrowhawk *A. brevipes* and the Chinese Sparrowhawk *A. soloensis*. Both breed in the Palearctic Region and are strongly migratory to Africa and Asia respectively (Ferguson-Lees & Christie 2001). The two other *Accipiter* species occurring in Madagascar, the Malagasy (Madagascar) Sparrowhawk *A. madagascariensis* and Malagasy (Henst's) Goshawk *A. henstii*, belong to other *Accipiter* clades (Wink & Sauer-Gürth 2004, JEMU unpublished).

MATERIAL AND METHODS

Collection and selection of samples for the molecular study (see Table 1)

During our ecological study of birds, blood samples of *A. francesiae* were obtained on Madagascar by L-AR, on Grand Comoro by MH, and on Mayotte by ML and MH. Feather samples were obtained on Mayotte by ML. Fresh tissue samples from Anjouan were not obtained because the subspecies is very rare. Toe pads were sampled for all races from specimens stored in the RMCA and RBINS collections. For the tissue material obtained from the two related *Accipiter* species, see the Acknowledgments section.

Laboratory methods

Total genomic DNA was extracted from the toe pads of museum specimens, and from blood samples or feather shafts of living specimens, using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany) following the manufacturer's protocol. Overlapping fragments of approximately 100, 300, or 700 bp length of the COI gene were PCR-amplified. PCR was carried out using a TProfessional thermocycler (Biometra) in a reaction volume of 30 µl, containing 2 µl of genomic DNA, 3 µl of 10X PCR buffer, 0.2 mM dNTPs, 0.8 µM of each primer, 2.0 mM Mg-Cl₂, 0.5 U of Platinum Taq DNA polymerase (Invitrogen) and mQ-H₂O. The PCR profile was: 4 min at 94°C followed by 35 cycles of 30 s at 94°C, 30 s at 50°C and 45 s at 72°C; with a final extension of

7 min at 72°C. Museum samples that failed in a first PCR attempt were redone with 4 µl of DNA added to the reaction mix and with 40 PCR cycles. In order to avoid contamination, aerosol barrier tips and different rooms for pre- and post-PCR steps were used. All PCR products were visualized with the E-Gel Electrophoresis System (Invitrogen). PCR products were purified using the NucleoFast 96 PCR Plate kit (Macherey-Nagel, Germany) and sequenced using the BigDye Terminator v1.1 chemistry on an ABI 3130xl automated capillary DNA sequencer (Applied Biosystems). Sequences were checked, assembled, and aligned in SeqScape v2.5 (Applied Biosystems).

Whenever possible we used the BirdF1d and BirdR1d degenerated primers modified after Hebert *et al.* (2004) and Lohman *et al.* (2008) for the standard DNA barcode region (694 bp in birds) (Table 2). For museum specimens, we used BirdF1d and BirdH351d to amplify a 298 bp DNA fragment corresponding to the first half of the standard DNA barcode, and BirdF1d and BirdH153d to amplify a 100 bp DNA fragment representing the first part of the standard DNA barcode (Table 2). This "mini-barcode" region corresponds to the first 100 bp of the universal DNA mini-barcode (128 bp) proposed by Meusnier *et al.* (2008). For the second half of the DNA barcode we used the primers L288_310dt or L501_523dt with BirdR1dt amplifying a 434bp and 224 bp fragment with the same PCR protocol as for the other primer combinations.

TABLE 1. Samples of *Accipiter francesiae* and both outgroups used in this study with geographical coordinates. Geographical coordinates marked with an asterisk are estimated from locality names on collection labels. #: partial sequence obtained, sample not used in the analyses; ##: migratory bird, no information on source or destination population.

(Sub)species	Country/island	Haplo-type	GenBank accession number	Geographical coordinates	Tissue used
<i>A. f. francesiae</i>					
RBINS35415	Madagascar	ht1	JF312086	18°55'S_47°33'E*	toepad
RBINS35416	Madagascar	ht1	JF312104	18°55'S_47°33'E*	toepad
RMCAA90380001	Madagascar	ht1	JF792344	14°19'42"S_48°34'54"E	blood
RMCAA90380002	Madagascar	ht1	JF792345	15°28'42"S_48°28'00"E	blood
RMCAA90380003	Madagascar	ht1	JF792346	15°28'42"S_48°28'00"E	blood
RMCAA90380004	Madagascar	ht1	JF792347	15°59'00"S_47°56'18"E	blood
RMCAA90380005	Madagascar	ht2	JF792348	15°37'48"S_49°58'30"E	blood
RMCAA90380006	Madagascar	ht1	JF792349	18°15'06"S_49°17'54"E	blood
RMCAA90380007	Madagascar	ht1	JF792350	18°13'24"S_49°18'48"E	blood

TABLE 1. Continued.

(Sub)species	Country/island	Haplo- type	GenBank accession number	Geographical coordinates	Tissue used
<i>A. f. brutus</i>					
RMCAA8_17_A_1	Mayotte (Comoros)	ht7	JF312162	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_2	Mayotte (Comoros)	ht7	JF312172	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_3	Mayotte (Comoros)	ht7	JF312174	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_5	Mayotte (Comoros)	ht7	JF312175	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_6	Mayotte (Comoros)	#	JF312176	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_7	Mayotte (Comoros)	ht8	JF312177	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_8	Mayotte (Comoros)	ht7	JF312178	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_9	Mayotte (Comoros)	ht7	JF312179	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_10	Mayotte (Comoros)	ht8	JF312163	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_11	Mayotte (Comoros)	ht7	JF312164	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_13	Mayotte (Comoros)	ht7	JF312165	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_14	Mayotte (Comoros)	ht7	JF312166	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_15	Mayotte (Comoros)	ht8	JF312167	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_16	Mayotte (Comoros)	ht8	JF312168	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_17	Mayotte (Comoros)	ht7	JF312169	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_18	Mayotte (Comoros)	ht7	JF312170	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_19	Mayotte (Comoros)	ht8	JF312171	12°49'30"S_45°08'00"E	feather
RMCAA8_17_A_20	Mayotte (Comoros)	ht7	JF312173	12°49'30"S_45°08'00"E	feather
<i>A. f. griveaudi</i>					
RMCA8343A199	Grand Comoro	ht5	JF312093	11°39'17"S_43°19'13"E*	toepad
RMCAAfran006	Grand Comoro	ht5	JF312100	11°48'S_43°16'E	blood
RMCAAfran007	Grand Comoro	ht5	JF312101	11°48'S_43°16'E	blood
RMCAAfran008	Grand Comoro	ht5	JF312102	11°48'S_43°16'E	blood
RMCAAfran009	Grand Comoro	ht5	JF312103	11°48'S_43°16'E	blood
RMCAAcc006	Grand Comoro	ht5	JF312096	11°48'S_43°16'E	blood
RMCAAcc007	Grand Comoro	ht5	JF312097	11°48'S_43°16'E	blood
RMCAAcc008	Grand Comoro	ht4	JF312098	11°48'S_43°16'E	blood
RMCAAcc010	Grand Comoro	ht3	JF312099	11°48'S_43°16'E	blood
RMCAAcc011	Grand Comoro	#	JF312189	11°48'S_43°16'E	blood
<i>A. f. pusillus</i>					
RMCA8343A358	Anjouan (Comoros)	ht6	JF312094	12°12'49"S_44°26'13"E*	toepad
LI1941/662	Anjouan (Comoros)	#	JF312095	12°12'49"S_44°26'13"E*	toepad
RBINS8867	Anjouan (Comoros)	#	JF312089	12°11'S_44°43'E	toepad
<i>A. brevipes</i>					
RMCAAcc235	Israel	##	JF312109	bird migrating	blood
<i>A. soloensis</i>					
RMCAA90081	South Korea		JF312181	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90082	South Korea		JF312182	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90083	South Korea		JF312183	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90084	South Korea		JF312184	34°41'47.66"N_125°11'54.10"E	feather
RMCAA90085	South Korea		JF312185	37°26'42.37"N_127°16'34.39"E	feather

TABLE 2. Primer combinations used in this study.

Primer combination	Forward primer sequence	References forward primer	Reverse primer sequences	References reverse primer	Fragment length (bp)
BirdF1d+Bird_H153_175d	TCAACCAACCACAAAGAVATYGGYAC	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	ACGATTACRTTGTARATYTGRTG	This study	100
BirdF1d+Bird_H351_370d	TCAACCAACCACAAAGAVATYGGYAC	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	CCTGCTCCWGGCTTCTAYDGT	This study	298
BirdF1d+birdR1dt	TGTAAACGACGGCCAGTTCAACCAACCACAAA-GAVATYGGYAC	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	CAGGAAACAGCTATGACACGTGGGAGATGATT-CCGAAKCKGG	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	694
Aves_L288_310dt+birdR1dt	TGTAAACGACGGCCAGTCGCATAAAYAACATA-AGCTTYTG	This study	CAGGAAACAGCTATGACACGTGGGAGATGATT-CCGAAKCKGG	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	424
Aves_L501_523dt+birdR1dt	TGTAAACGACGGCCAGTACGGCCATCAACATA-AAACCNCC	This study	CAGGAAACAGCTATGACACGTGGGAGATGATT-CCGAAKCKGG	modified from Hebert <i>et al.</i> 2004, Lohmann <i>et al.</i> 2008	224

For all samples, except RBINS 8867 (100 bp fragment only), we successfully sequenced at least the 298 bp fragment. Sequences are available in GenBank (see Table 1).

Phylogenetic inference and network analysis

Neighbor-Joining (NJ) analysis on K2P distances (Kimura 1980) and parsimony analysis were run using PAUP* v.4b10 (Swofford 2002). One thousand bootstrap replicates served for testing branch support. Maximum likelihood analysis was conducted in Garli v0.96 (Zwickl 2006), running two searches and with 200 bootstrap replicates. Nucleotide substitution models for parsimony and maximum likelihood analyses were selected in jModelTest (Posada 2008) applying the AIC(c) and BIC criteria. Two other reptile-eating raptors, *A. brevipes* (Acc 235) and *A. soloensis* (RMCA A90082, RMCA A90083, RMCA A90084, RMCA A90085), were used as outgroups; *A. soloensis* is the closest relative (unpublished data) of *A. francesiae* and *A. brevipes* is an African representative of the genus.

Because part of the material was old (> 20 years) the full (694 bp) barcode fragment could not be sequenced. Therefore the analyses were performed on a data set of the first 572 bp of the barcode fragment. A median-joining haplotype network was constructed using Network v4.5.1 (<http://www.fluxus-engineering.com>) with default settings (Bandelt *et al.* 1999).

RESULTS

Including both outgroups, the 572 bp fragment yielded 87 variable sites, of which 41 were parsimony informative. Within *A. francesiae* there were 14 variable sites, of which eight were parsimony informative. Eight haplotypes were found in *A. francesiae* which appeared to be monophyletic (Fig. 2). Within *A. francesiae* two groups were found, although one group only showed high bootstrap support for the NJ analysis. One group comprises the two haplotypes of *A. f. francesiae* from Madagascar, one of which is probably common (eight individuals) and widespread whereas the other haplotype was found in a single individual in our data set. The second group comprises the haplotypes from the Comoros. Two out of the three haplotypes of *A. f. griveaudi* were single individuals and six other specimens belonged to a third haplotype. Also two haplotypes were found in *A. f. brutus* (Table 1). Despite the limited number of sampling localities on both Grand Comoro and on Mayotte (their coordinates are given in Table 2), specimens with different haplotypes were found syntopically on both islands. For *A. f. pusillus* we could only successfully sequence the long fragment from a single individual (toe pads from other specimens yielded short fragments; Table 1). Even though the haplotypes of *A. f. brutus* and *A. f. griveaudi* grouped together, the nodes had low bootstrap support (i.e. between 60 and 70%) (Fig. 2). A median-

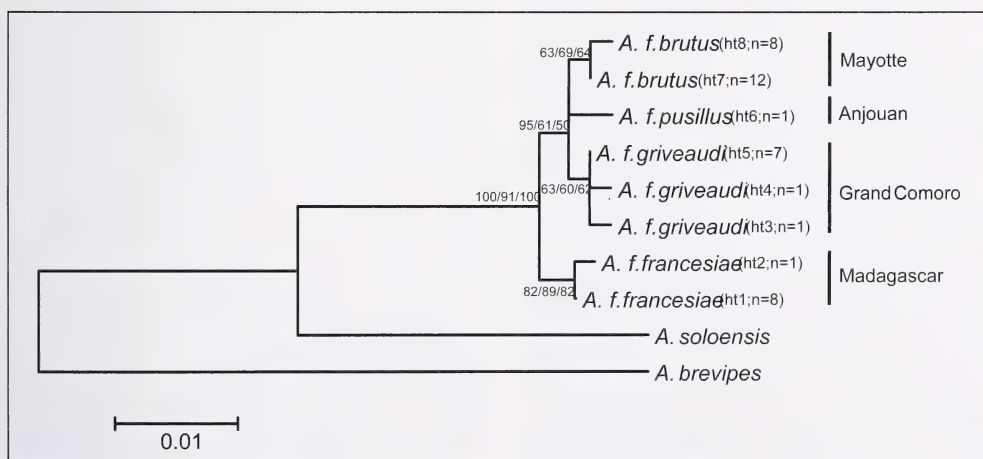


FIG. 2. Phylogenetic tree with indication of major lineages of eight COI haplotypes (ht1–ht8; n = number of individuals) of *Accipiter francesiae* and two outgroup taxa. Bootstrap values for node support are shown on the branches: neighbour-joining (1000 replicates) / maximum likelihood (200 replicates) / parsimony (1000 replicates). Bootstrap values $\geq 50\%$ are shown. Branch lengths are according to the NJ tree.

joining haplotype network is presented in Fig. 1 and shows that all islands have different haplotypes of *A. francesiae*.

DISCUSSION

Our phylogeographic analysis based on the COI gene shows that *A. f. francesiae* from Madagascar appears well-differentiated from the other subspecies and that these other subspecies are less differentiated. Yet even though the genetic differences between the Comoran subspecies are very small, each subspecies corresponds to one or more unique mitochondrial haplotypes and none of the haplotypes is shared between subspecies. It may thus also be assumed that there is little, if any, exchange of individuals between different islands. Surprisingly, on the one hand, the two well-studied *A. francesiae* Comoro populations (Mayotte and Grand Comoro), resident on small oceanic islands, show some within-island molecular variation, notwithstanding rather small potential and actual (confirmed in the case of Grand Comoro) population sizes. On the other hand, we only found two haplotypes (h1: eight individuals; h2: one individual) in *A. f. francesiae* on Madagascar, despite the larger geographical sampling (Fig. 3).

Interestingly, in contrast to the limited molecular differentiation, the subspecies differ markedly in morphology. In birds, isolation on islands is known to lead to rapid changes in morphology when compared to their mainland source population (Burns *et al.* 2002, Mathys & Lockwood 2009). This finding could be due to different (or new/absent) selection pressures such as the absence of (or the presence of other) predators, competitors and pathogens, and/or the availability of new niches in the new habitat (Ricklefs & Birmingham 2007, Clegg *et al.* 2008), or it may be the result of founder effects due to limited genetic variability in (presumably small) founder populations.

Accipiter francesiae is listed in the category “least concern” according to the IUCN Red List (BirdLife International 2009). However it is current practice to also consider intraspecific variation in conservation strategies. Because the subspecies of *A. francesiae* i) are morphologically differentiated, ii) each consist of a number of unique mitochondrial haplotypes, and iii) appear strongly isolated from each other, they may each represent independent evolutionary units. In that case, conservation efforts should focus on each of the subspecies. This focus should apply to *A. f. pusillus* in particular, which is very rare. Extinction

of this subspecies would result in a significant loss of intraspecific genetic variation (i.e. a unique mitochondrial haplotype and morphological variation) in this sparrowhawk.

The small genetic differences suggest a relatively recent colonization of the Comoros. Furthermore, the molecular pattern indicates that these islands were colonized within the same historical timeframe. It can tentatively be assumed that the colonization occurred from north Madagascar, which is a scenario that has been found in several terrestrial vertebrate taxa such as night-geckos (Jackman *et al.* 2008), day-geckos (Rocha *et al.* 2009), and frogs (Vences *et al.* 2003). Louette (2004), in an overview of colonization patterns for the birds of the Comoros, sug-



FIG. 3. Map of Madagascar. Black pins indicate sampling localities of individuals with haplotype 1 (ht1). Note that at some localities more than one individual was sampled; the white pin indicates the sampling locality of the individual with haplotype 2 (ht2). For the geographical sampling coordinates we refer to Table 1.

gested that birds evidently disperse more readily than geckos and frogs, as indicated by the number of bird taxa shared among the islands, although the direction of colonization has not been proven. The same holds for *A. francesiae*. For instance, there is a minimum of four mutational steps between *A. f. francesiae* (Madagascar) and *A. f. griveaudi* (Grand Comoro) or *A. f. brutus* (Mayotte), but the same number of mutational steps occurs between haplotypes from the Comoro subspecies. Nevertheless, the Comoran subspecies probably share a common ancestor (Fig. 1) that is younger than the common ancestor of the Malagasy and Comoran clades. However, the limited number of specimens for some of the subspecies, and the limited variation in the COI gene, do not allow speculation on the exact colonization route or divergence times, although the low variation suggests a recent split between the subspecies.

A large-scale molecular analysis of the genus *Accipiter* is currently ongoing. Preliminary results show that, in general, genetic divergences of mitochondrial gene markers among *Accipiter* species are small (Van Houdt *et al.* 2009, JEMU unpublished data) suggesting a rapid radiation within this genus. Nevertheless, the analysis will shed light on the relationship between *A. francesiae* and the other *Accipiter* species and provide information on the colonization of western Indian Ocean islands (e.g. Comoros and Madagascar) by this species. The western Indian Ocean islands have been considered as part of the African realm (see Newton 2003), but the fauna on these islands is in fact a mixture of both old African and Asian clades (Keith 1980, Louette 1996, Hawkins & Goodman 2003). This situation has been demonstrated in detail for the bulbuls genus *Hypsipetes*, which is shared with, and derived from, Asia (Louette & Herremans 1985, Warren *et al.* 2005). However, this is not a general rule. Warren *et al.* (2003) concluded an African origin for the genus *Nectarinia*. For other genera, such as *Zosterops*, *Dicrurus*, and *Otus*, Warren *et al.* (2006), Pasquet *et al.* (2007), and Fuchs *et al.* (2008) respectively postulate complex dispersal histories from both continents. These authors even mention the possibility of an island being a source for the colonization of a continent. Bellemain & Ricklefs (2008) have discussed cases of continents being colonized from islands in other parts of the world. Although we do not consider this possibility likely in the *A. francesiae* Madagascar ("continent") - Comoros (island) case, we cannot refute it.

Interestingly, in our analyses of *Accipiter* data sets (containing the vast majority of the African representatives, JEMU unpublished), *A. soloensis* from Asia groups as the closest relative of *A. francesiae*. It is thus a possible scenario that the ancestor of *A. soloensis*, which occurs on migration in SE Asia (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001), made an overshoot migration to Madagascar in the distant past and may have settled in the Madagascar area after loss of migratory behavior. This theory was hypothesized for some related buteonine hawks, in which a number of island colonizers turned sedentary (Raposo do Amaral *et al.* 2009). Another famous example among raptors is the Palearctic migrant Short-toed Eagle *Circus gallicus* that settled in Wallacea (White 1976).

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